Consecutive cohort effects driven by density-dependence and climate influence early-life survival in a long-lived bird

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Abstract

Conditions during early life, including maternal cohort effects, can influence the future fitness of individuals. This may be particularly true for long-distance migrating birds, because, apart from conditions experienced by cohorts during rearing, conditions during early-life in regions far from breeding grounds may also influence their population dynamics. Very little is known about the fitness consequences of those conditions experienced by juveniles after independence, especially in wild populations and for long-lived birds. We used multi-event capture-recapture-recovery models and a unique 26-year dataset for the Audouin's gull (*Larus audouinii*) to assess for the first time whether survival was influenced by early conditions, both during the rearing period (i.e., a maternal cohort effect potentially affected by density-dependence) and the first winter (i.e., a cohort effect driven by climate when birds disperse to wintering grounds). Our results show that juvenile survival was highly sensitive to early-life conditions and that survival decreased with stronger density-dependence and harsh climate. The two consecutive cohort effects were of similar magnitude and they may represent a selection filter. Thus, early-life conditions had a strong impact on survival, and neglecting this complexity may hinder our understanding on how populations of long-lived animals fluctuate and respond to perturbations.

Keywords:

Early-life conditions; survival; long-lived seabird; first year; density-dependence; winter.

1. Introduction

Conditions during early life can determine an individual's future fitness [1]. Those conditions are known as cohort or silver-spoon effects and have been widely explored on a large range of vital rates in many taxa (see the electronic supplementary material S1, [2–5]). Individuals facing harsh early-life conditions are expected to experience higher fitness costs later in life [1]. Harsh conditions include unfavourable climate, high population size, low habitat quality, poor parental quality and low food availability, and their potential interaction (see the electronic supplementary material S1, [2–5]). The ability of offspring to compensate for a poor start in life determines whether early-life conditions have short- or long-term fitness consequences [6–8]. The former, also known as numerical effects, involves changes in traits such as pre-breeding survival, birth weight, birth date and body growth; the latter, known as delayed quality effects, affects future breeding performance and thus results in changes in the age of first breeding attempts, lifetime reproductive success and adult survival [2–5,9–13]. Environmental forcing in early life drives complex trade-offs between vital rates and thus, many of the effects noted above are likely to be interrelated [10,14]. Overall, early-life conditions may generate differences in vital rates between cohorts and can have important demographic consequences. For instance, cohort differences may result in delays in a population's response to environmental conditions that could destabilize its population dynamics [1].

Comparatively, far more attention has been directed at explaining the effects of early-life conditions on reproduction rather than on survival [10,15]. Within survival studies, substantial research describes the effects of early-life conditions under controlled experimental conditions [3,16] but much less is known about wild populations of long-lived species [3,13,16]. Additionally, it is likely that the processes underlying the strong early-life selection pressures on survival, which lead to high and stable adult survival rates in long-lived species, are not limited to the rearing period [17]. For example, conditions experienced during winter may give rise to important changes in demographic rates such as recruitment, dispersal and even survival [18]. Nevertheless, winter conditions have been seldom considered as a type of cohort effect, even though these conditions may primarily affect juveniles. Thus, first-winter conditions are likely to play a key role in the dynamics of natural populations, and their integration into early-life condition studies should therefore be considered. Yet, in some long-lived

73 species and particularly in birds, juvenile stages are often elusive and information about
74 critical periods other than the breeding period is scarce [19].

75 Here, we explore the potential survival costs of a bad start in life in a long-lived bird,
76 the Audouin's gull (*Larus audouinii*). We tested the survival costs associated with the
77 conditions experienced by individuals during two critical early-life periods: the rearing
78 phase and their first winter. Food is a key factor shaping population dynamics. Density-
79 dependence and climate, which regulate food availability, are likely to be crucial during
80 these two life phases [20]. We predicted that individuals belonging to cohorts
81 experiencing harsh environmental conditions during its first year (i.e., low food
82 availability during both rearing and wintering periods) would endure greater survival
83 costs later in life. In addition, we predicted that, since the study species is a long-lived
84 bird, these effects would be strong in the first years of life and weak or non-existent on
85 adult survival [7,19].

86 **2. Methods**

87 (a) Demographic data
88 We collected demographic data in Punta de la Banya (Ebro Delta, Spain; 40º37' N,
89 00º35' E), a flat sandy peninsula of ca. 2600 ha. The site holds ca.60% of Audouin's
90 gull's world population [21]. During 1988–2012 a total of 24 038 chicks were
91 individually marked at fledging using a plastic band with a unique alphanumeric code.
92 A total of 33 322 resightings and 552 recoveries were used in the analyses. Resightings
93 were made during the breeding season (April–July) using spotting scopes. Recoveries of
94 dead birds took place at the study site (authors' own fieldwork) and abroad (information
95 provided by ringing offices).
96
97 (b) Environmental data
98 We tested whether survival was affected by conditions experienced during the rearing
99 period and after independence, during the first winter along the NW African coast. As a
100 proxy of rearing conditions we used food availability per capita[22,23]. Audouin's gull
101 is a long-lived seabird that breeds colonially from April to July and usually lays three
102 eggs. The species feeds mainly on small pelagics [24], and discards from trawling fleets
103 can represent up to 75% of their diet during the breeding season [25]. In the study area,
104 La Ràpita is the most important fishing harbour and accounts for 60% of the catch in

number and 74% in total power. Thus, we took trawling landings at La Ràpita as a proxy of food availability in June, when chicks are under parental care. We then divided this proxy of food availability by population size of both Audouin's and Yellow-legged gulls (*L. michahellis*), the most abundant sympatric species that exploits discards [25], to account for density dependence of the guild through interference competition and obtained the proxy of food availability per capita (hereafter DD). As a proxy of first winter conditions, we used the North Atlantic Oscillation climatic index during December–March (hereafter W_{NAO}), because gulls disperse during winter mostly to the Senegambia region [26]. This long-distance dispersal decreases with age, and most birds do not cross to Africa as they become older (figure 1) [26]. High positive W_{NAO} values are associated with the intensification of upwelling and thus with higher small pelagic fish availability [27]. DD and W_{NAO} index are independent of each other (R^2 = 0.011, p = 0.636).

(c) Modelling and hypothesis testing

Models were constructed in a multi-event capture-recapture framework, which addresses state uncertainty by relating the true state of the individual to the observed event via a series of conditional probabilities [28]. Goodness of fit test (GOF, see the electronic supplementary material S2) suggested the presence of both trap-dependence and transience effects. After accounting for them, an acceptable variance inflation factor of 1.42 was obtained and used to correct all models constructed in E-SURGE [29,30]. Based on the GOF results we built models with four states (Aa, alive and trap-aware; Au, alive trap-unaware; Dr, recently dead and Dl, dead long ago) and three events (0, not seen; 1, seen alive and 2, seen dead) (see the electronic supplementary material, S3). We used previous knowledge of the species [34–36] to design our initial exploratory set of models and select the best general model structure based on QAICc criterion (see the electronic supplementary material S4.1)[34]. We tested the absence of long-term cohort effects by running additive and interaction models including cohort and age effects. Once confirmed, we used the best general model to run different models including the effect of DD and W_{NAO} in early-life and their additive and interaction effects. Finally, we calculated the fraction of temporal variation explained by each covariate (DD and W_{NAO}) using ANODEV [35](see the electronic supplementary material, S5). This was first tested in the general model with the best age structure and then in each of the young age-classes in order to evaluate their temporal extent.

3. Results

The best recapture structure retained three age classes with different recapture probabilities, time and a trap awareness effect (STEP1, see the electronic supplementary material S4.1). The model including temporal variation in recovery probabilities performed the best (STEP2, see the electronic supplementary material S4.1) and the best structure for survival included five age classes with an interaction with year (STEP3, see the electronic supplementary material S4.1 and S4.2 for model estimates, figure 2). We also evaluated the potential effects of early-life environmental covariates on survival. Models including DD and W_{NAO} covariates performed poorly in terms of QAICc compared to the best model, the time varying model (see the electronic supplementary material S4.3), but they explained large proportions of survival variability. DD explained 34 % of survival variability, W_{NAO} explained 17 % of survival variability, and the models including additive and interaction effects explained 42% and 50% of survival variability respectively (see the electronic supplementary material S4.3, all $p \leq 0.002$).

Once the effect of both DD and W_{NAO} had been confirmed, we evaluated their effects on each of the five ages considered. DD and W_{NAO} had a strong influence on Audouin's gull survival but the effect faded after the first year of life (beta estimates β (and 95% confidence intervals CI) for first-year survival φ_1: $\beta_{DD} = 0.625$ (0.248, 1.001), $\beta_{WNAO} = 0.464$ (0.376, 0.551) see the electronic supplementary material S4.4 showing beta estimates for each model). Offspring born under high food availability per capita and those that experienced mild first winters (high W_{NAO} values) had increased first-year survival rates. DD and W_{NAO} explained similar amounts of survival variability — about 50% of first-year survival ($p = 0.000$; see figure 3 and the electronic supplementary material S4.5). The model including both DD and W_{NAO} conditions explained a significant 62% of first-year survival ($F_{2, 19} = 15.52$, $p < 0.001$, see the electronic supplementary material S4.5). Models including an interaction effect do not explain any extra variance compared to the models including only the additive effect.

4. Discussion

Several previous studies show that the effects of early-life conditions on fitness components can be important: the harsher the conditions an individual experiences during early life, the higher fitness costs the individual will undergo [1,3,4,6]. However,

few studies have attempted to unravel the fitness consequences of early-life conditions in critical periods other than the rearing period, especially in wild populations [3]. We evaluate for the first time both the effects of early-life conditions experienced during rearing, but also during the first winter on the survival of a long-lived bird. Here, we find that both rearing and first winter conditions influenced first year survival. Although harsh early-life conditions can have consequences for long-term fitness, their influence is usually most pronounced during early life stages [1,10]. We also show here that in Audouin's gulls, harsh early-life conditions strongly influenced first-year survival but that influence fades at older ages. The mechanisms driving trade-offs of poor early-life conditions in future fitness are likely to respond to complex causal routes and they remain fairly unknown. Thus, we cannot ascertain whether what we observed was the result of compensatory effects, acquired resilience, life history trait plasticity or a combination of those processes [10,36]. Previous studies suggest that early-life conditions might act as selection filters by eliminating frail individuals from the population, and leading to stabilization of adult survival at high values by environmental canalization typical for long-lived species [14,37–39]. Our results suggest that a strong selection filter operate on this species at least during the first year of life, eliminating those frail individuals, and the strength of mortality during this period depends on the severity of environmental conditions during early life. Therefore, rearing and first winter periods seem to be operating as two consecutive cohort effects likely resulting in a positive selection for high-quality phenotypes [17].

In our study, food competition by density-dependence was a key factor driving the effects of early-life conditions on survival. Breeding gulls intensively exploit trawler fleet discards, and food availability per capita during the rearing period is positively related to improved chick body condition and higher reproductive success [25,40]. We show here that food availability per capita for breeders during rearing also improves future survival of newborns. This cohort effect during the rearing period can be considered a maternal effect because the environment experienced by the mothers influences the future performance of their offspring. After fledging, juveniles disperse and winter in the Senegambia region, where they mainly feed on small pelagic fish shoals [26]. Climatic conditions during first winter also influenced juvenile survival. Positive NAO is associated with the strengthening of the African Coast upwelling and increasing the availability of small pelagics [41–43]. Therefore, higher food availability during first winter period improves juvenile survival. Our results agree with our

204 expectations on the survival components of fitness; that is, individuals suffering from
205 food limitation during their early life, both during rearing and first winter, suffer fitness
206 costs [44].

207 We found that individuals born in years when there was lower competition for
208 foraging resources survived better in their first year of life. When individuals attempt to
209 exploit a common limited resource, competition occurs [45]. The degree of competition
210 depends on both the absolute resource availability and the number of individuals
211 exploiting that resource. Hence, this is a density-dependent process [45,46].
212 Competition is common in natural populations and so its effect is implicitly accounted
213 for in most early-life condition studies [16,44]. Such studies include either population
214 size or resource availability as competition proxies and many have found strong
215 density-dependent effects for different fitness components [47–49]. However, we
216 suggest that, when available, the combination 'resource availability per capita' is likely
217 to be a more accurate proxy for density-dependence driven by competition. Density-
218 dependent effects on juvenile survival have been widely reported, especially in
219 mammals and birds [2,3,16,50]. These studies suggest that this demographic trait and,
220 particularly, first-year survival are the most affected by density-dependence. However,
221 these survival rates are also likely to be the most variable over the years since they have
222 not been environmentally canalized.
223 Environmentally induced responses are often complex and lead to covariance
224 processes within demographic traits [51,52]. For instance, a decrease in density-
225 dependence during rearing increased not only survival rates of gulls (our study), but
226 also the reproductive performance of breeders [22]. These variations in how individuals
227 from different cohorts respond to environmental conditions act as a structuring force in
228 population dynamics, because cohorts of individuals might differ considerably in their
229 future performance [53,54]. The influence of age and environmental variability over the
230 years on several life-history traits and population dynamics has been extensively studied
231 in many taxa, but the potential influence of cohort effects has been seldom considered
232 [55]. For instance, a cohort of individuals reaching sexual maturity synchronously and
233 beginning to breed in a harsh reproductive season can pay a reproductive cost with
234 reduced survival and lifetime reproductive success. Furthermore, the next cohort of
235 offspring could inherit the effects of this bad maternal environment. Thus, we highlight
236 here the relevance of monitoring early-life phases for understanding their sensitivity to

environmental conditions and the potential consequences for population dynamics. Although life-history theory predicts that adult survival will be the key parameter driving population functioning, juvenile survival has recently been acknowledged as an important source of variability in population dynamics [17,37,49].

Here, we present the first evidence on how both rearing and first winter conditions shape the survival of the first year of life via density-dependence and climate effects. These two consecutive cohort effects synchronously influence the survival of individuals born in the same season and suggest the existence of delayed life-history effects, such as variability and delay in density-dependence in population dynamics [54]. The incorporation of these findings into fitness studies and future population models will provide a better understanding of complex population dynamics.

Author contributions

APP, MG, AB & DO collected the data; DO conceived the idea, APP & RP conducted the analyses, APP led the writing and APP, MG, AB, RP and DO co-wrote the article.

Ethics statement

This study complies with the current European and Spanish laws regulating scientific research on animals. Permits were given by Spanish Ministry of the Environment and Delta de l'Ebre NP.

Data accessibility

Data available from the public CEDAI Repository: http://cedai.imedea.uib-csic.es/geonetwork/srv/es/main.home?uuid=e13d37f4-2fe6-4f9e-8a51-d60bc6ea1a2c

Competing interests

We have no competing interests.

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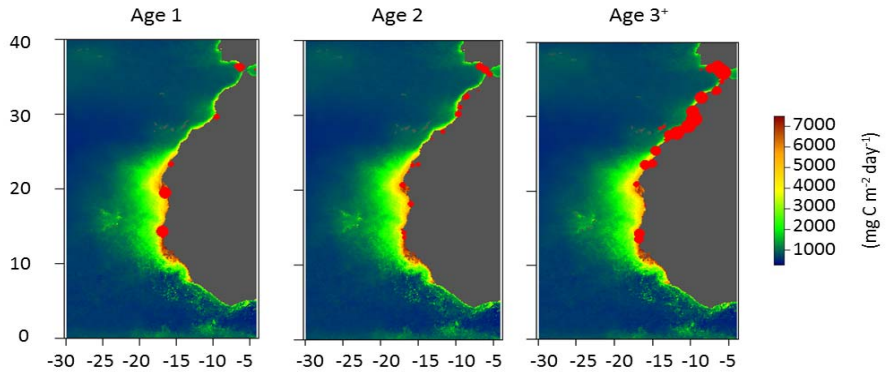
436 FIGURES

437 **Figure 1.** First winter conditions for Audouin's gulls, expressed as the average winter
438 net primary production during 2002–2012 (mg C m^{-2} day^{-1}) on the Northwest African
439 coast, which influenced the availability of small pelagics. Left panel represents first
440 winter resightings of animals marked at the Ebro Delta (red dots), whereas right panels
441 show those resightings for older birds (red dots). The size of red dots is proportional to
442 the number of individuals resighted. Resighting data were provided by the Catalan
443 Ringing Office (www.ornitologia.org).



444

445 **Figure 2.** Annual survival (95% CI) of Audouin's Gulls breeding in the Ebro Delta in
446 1988–2012 (each panel represents one of the five age classes retained by the best model;
447 see the electronic supplementary material S4.1).

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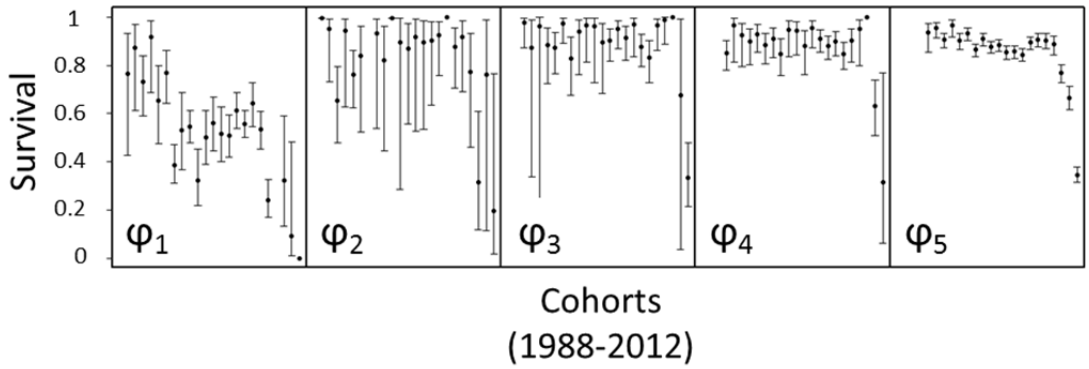

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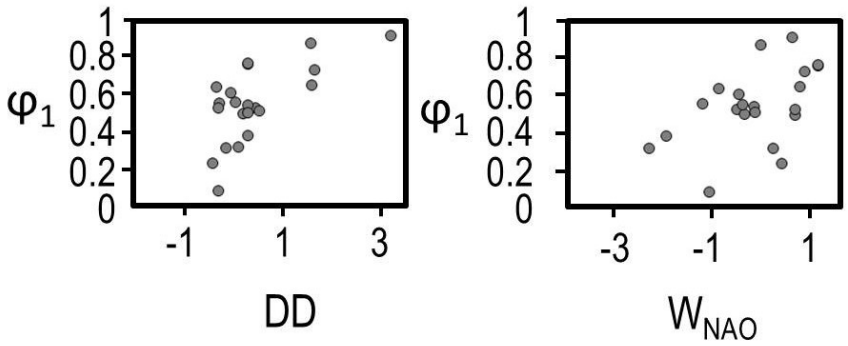
451 **Figure 3**. Relationship between first year survival (φ_1) of Audouin's gulls breeding in
452 the Ebro Delta and tonnes of fish landed by trawlers per capita, including Audouin's
453 and yellow-legged gulls (DD); and W_{NAO}, Northern Atlantic Oscillation index, during
454 the first winter of life.



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